

Infant carrying behaviour in dolphins: costly parental care in an aquatic environment

S. R. Noren*

Institute of Marine Science, Center for Ocean Health, University of California at Santa Cruz, 100 Shaffer Road, Santa Cruz, CA 95060, USA

Summary

1. Infant carrying behaviour occurs across diverse taxa inhabiting arboreal, volant and aquatic environments. For mammals, it is considered to be the most expensive form of parental care after lactation, yet the effect of infant carrying on the energetics and performance of the carrier is virtually unknown.
2. Echelon swimming in cetacean (dolphin and whale) mother–infant dyads, described as calf in very close proximity of its mother's mid-lateral flank, appears to be a form of aquatic 'infant carrying' behaviour as indicated by the hydrodynamic benefits gained by calves in this position which enables them to maintain proximity of their travelling mothers. Although this behaviour provides a solution for minimizing separations of mother–infant dyads, it may be associated with maternal costs.
3. Through kinematic analyses this study demonstrates empirically that 'infant carrying' impacts the locomotion of dolphin (*Tursiops truncatus*) mothers as evident by decreased swim performance and increased effort.
4. The mean maximum swim speed of mothers swimming in echelon only represented 76% of the mean maximum swim speed of these mothers swimming solitarily. In addition, there was a concomitant 13% reduction in distance per stroke for mothers swimming in echelon compared to periods of solitary swimming.
5. Thus, 'infant carrying' in an aquatic environment is associated with maternal costs, and could ultimately impact maternal energy budgets, foraging efficiency and predator evasion.

Key-words: cetacean, echelon position, hydrodynamics, kinematics, swimming

Introduction

Maternal investment in mammals includes gestation, lactation and other forms of parental care. Infant carrying is considered to be the most costly form of parental care after lactation (Altmann & Samuels 1992; Kramer 1998) and has been described in 6 of 19 eutherian mammalian orders (for review, see Ross 2001). This behaviour provides a solution for mothers of diverse taxa that must manoeuvre within their environment to forage and avoid predators while accompanied by their young offspring (Ross 2001), which are handicapped by small body size, undeveloped tissues and naïveté (Carrier 1996). This behaviour is only thought to evolve when offspring are unable to independently follow their mothers, as in arboreal (i.e. primates) and volant (i.e. bats) environments (Ross 2001).

The aquatic environment also appears to require 'infant carrying' to ensure that mother–infant dyads remain intact during travel as manatees and sea otters are observed physically carrying their young. Cetaceans (whale and dolphin), however, cannot physically carry their young. Yet similar to that observed for primates (Altmann & Samuels 1992; Doran 1992; Wells & Turnquist 2001), mature locomotor performance in dolphins is precluded for several years postpartum (Noren, Biedenbach & Edwards 2006). Echelon position is the predominant behaviour displayed by cetacean mother–infant dyads (Fig. 1; McBride & Kritzler 1951; Tavalga & Essapian 1957; Norris & Prescott 1961; Au & Perryman 1982; Taber & Thomas 1982; Mann & Smuts 1999; Noren & Edwards 2007) and appears to represent an aquatic form of 'infant carrying' because it enables neonatal cetaceans to maintain close proximity to their mothers during travel (Norris & Prescott 1961; Lang 1966) by increasing the swimming efficiency of the infant (Kelly 1959; Weihs 2004; Noren *et al.* 2008). Thus cetaceans, like primates, appear to 'carry' their young.

*Correspondence author. E-mail: snoren@biology.ucsc.edu



Fig. 1. Three bottlenose dolphin mother-calf pairs swimming in echelon position. Echelon position is described as calf in very close proximity with its mother's mid-lateral flank in the region near her dorsal fin. Photo © and courtesy of Dolphin Quest Hawaii.

Only a few studies have examined the energetic and locomotor consequences of infant carrying for the carrier, and these studies have focused on primates (Altmann & Samuels 1992; Schradin & Anzenberger 2001) and marsupials (Baudinette & Biewener 1998). Meanwhile the maternal consequences of infant carrying in other taxa and environments (i.e. volant and aquatic) remain unexplored. In view of this, I examined the kinematics of dolphin mothers swimming with their calf in echelon (Fig. 1) and swimming solitarily (> 1 m from their calf and all other dolphins) to elucidate the effect of 'infant carrying' on maternal locomotor performance and effort in an aquatic environment. The advantages gained by calves in echelon position are examined in the accompanying paper (Noren *et al.* 2008).

Materials and methods

Three captive bottlenose dolphin (*Tursiops truncatus*) mother-calf pairs housed at Dolphin Quest Hawaii provided a controlled experimental approach to investigate cetacean locomotor performance and effort (Fish 1993; Skrovan *et al.* 1999; Noren *et al.* 2006, 2008). Methodologies regarding the dolphin enclosure, placement of the SCUBA diver-videographer, and placement of the dolphins in the water column are described in detail elsewhere (Noren *et al.* 2008). Experimental swim sessions included both opportunistic (no reward) and directional swimming between two trainers (reward-based). Echelon swimming was recorded only when the mothers' calves were 0–34 days postpartum. Thus, the present study only provides details regarding the maternal costs of echelon for mothers with very young calves (0–34 days postpartum). Solitary swimming was recorded at several intervals 0–2 years past parturition. Thirty-three hours of swimming were recorded and 334 short 1–6 s video clips were extracted and digitized (Fig. 2). Clips were divided into two association categories: (i) echelon position (Fig. 1); and (ii) solitary swimming (mother > 1 m away from calf and all other dolphins). In all clips the mothers were continuously stroking.

A quantitative assessment of swim effort was obtained by calculating peak-to-peak fluke stroke amplitude and tailbeat oscillation frequency. Higher amplitudes and frequencies are associated with greater energy expenditure (Kooyman & Ponganis 1998). Normalized tailbeat frequency (ratio of tailbeat frequency to

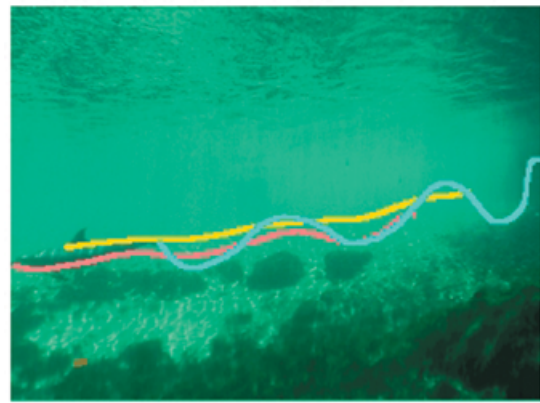


Fig. 2. A tracing from a digitized video clip of a solitarily swimming mother dolphin. Anatomical points of interest (rostrum tip, cranial insertion of the dorsal fin, and fluke tip) were digitized at a rate of 60 fields per second of video using a motion-analysis system (Peak Motus 6.1; Peak Performance Technologies, Inc. Englewood, CO, USA) following methods similar to Skrovan *et al.* (1999) and Noren *et al.* (2006). A distinct trace represents the movements of each digitized anatomical point. From left to right, the trace from the rostrum leads (pink), followed by the trace from the cranial insertion of the dorsal fin (yellow), and last is the trace from the fluke tip (blue). The brown dot is a digitized reference point indicating that the camera was steady while filming this video clip.

swim speed; Rohr & Fish 2004) and distance per stroke were also calculated. Methods for video analysis and swim effort calculations are described in detail elsewhere (Noren *et al.* 2006).

The goal of this study was not to address individual variation, but to quantify changes in locomotor performance associated with swim style (echelon vs. solitary), thus similar to other kinematic studies data across individuals were pooled (Fish 1993; Skrovan *et al.* 1999; Noren *et al.* 2006, 2008). Pearson product moment correlation coefficients were used to determine the correlations of peak-to-peak fluke stroke amplitude and tailbeat frequency with swim speed for echelon swimming and also for solitary swimming; linear regression analyses were then used to determine the relationship for the parameters that demonstrated a strong correlation. Swim speed, normalized tailbeat frequency, and distance per stroke during echelon swimming and solitary swimming were compared using student's *t*-tests when normally distributed, or Mann-Whitney rank sum tests when normality failed ($\alpha = 0.05$). The maximum swim performance of each individual during echelon swimming and solitary swimming was compared using a paired *t*-test ($\alpha = 0.10$). Statistical analyses were performed using SIGMA STAT 2.03 (Systat Software, Inc. Point Richmond, CA, USA). Means \pm 1 SEM are presented.

Results

Our experimental approach adequately captured swimming behaviours representative of wild dolphins (Noren *et al.* 2008). The average swim speed of mother dolphins was significantly slower during echelon swimming ($2.11 \pm 0.06 \text{ m s}^{-1}$; $n = 178$) than during solitary swimming ($3.88 \pm 0.09 \text{ m s}^{-1}$; $n = 156$; $T = 36534.00$, $P < 0.001$). Given that 53% of the echelon swim data were from directional swim trials, compared to 94% for the solitary swim data, swim speed data from directional trials only were also compared to ensure that the previous result was not due to experimental design. The result

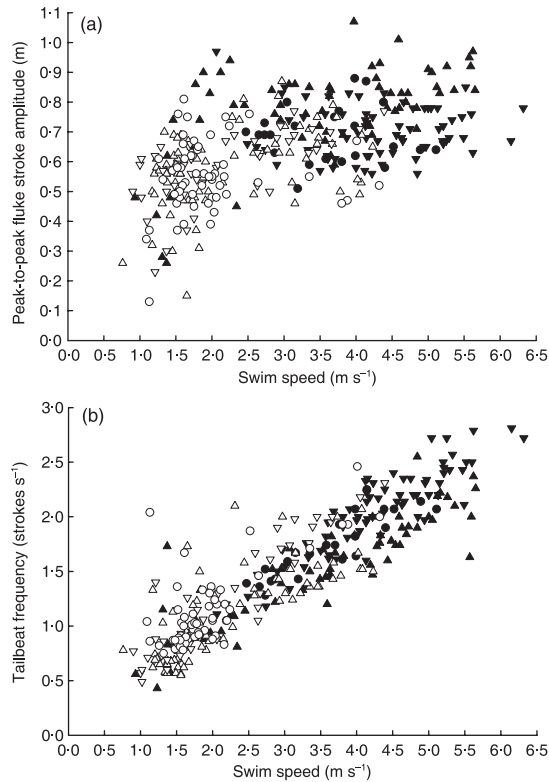


Fig. 3. Swimming kinematics of the mother in relation to the swimming speed of the mother. Peak-to-peak fluke stroke amplitude (a) and tailbeat frequency (b) were both correlated with swim speed for mother dolphins swimming in echelon with their calf (white symbols; $r = 0.400$, $P < 0.001$, $n = 178$ and $r = 0.799$, $P < 0.001$, $n = 178$, respectively) and swimming solitarily (black symbols; $r = 0.277$, $P < 0.001$, $n = 156$ and $r = 0.885$, $P < 0.001$, $n = 156$, respectively). The relationship between swim speed and peak-to-peak fluke stroke amplitude appears to be nonlinear. Given the strong linear correlation between swim speed and tailbeat frequency (SF) linear regressions are provided for echelon (speed = $1.61 \text{ SF} + 0.27$; $r^2 = 0.638$, $F = 310.794$, $P < 0.001$) and solitary (speed = $2.09 \text{ SF} + 0.13$; $r^2 = 0.783$, $F = 555.610$, $P < 0.001$) swimming. A different symbol is used for each of the three individual dolphins.

was the same; average swim speed during echelon swimming was significantly slower than during solitary swimming ($t = -11.644$, $P < 0.001$, $n = 94$, 145). The absolute maximum swim speed for each mother swimming with their calf in echelon was 4.23 , 4.39 and 4.32 m s^{-1} for animals 1, 2 and 3, respectively. This compares to 5.65 , 6.32 and 5.11 m s^{-1} for animals 1, 2 and 3 swimming solitarily, respectively. As a result, mean maximum swim performance was significantly slower when mothers were swimming in echelon ($4.31 \pm 0.05 \text{ m s}^{-1}$) compared to solitary swim periods ($5.69 \pm 0.35 \text{ m s}^{-1}$; $t = -4.816$, $n = 3$, $P = 0.053$).

Peak-to-peak fluke stroke amplitudes (Fig. 3a) and tailbeat frequencies (Fig. 3b) were correlated with swim speed for mother dolphins swimming in echelon and swimming solitarily. Because average swim speed was significantly different between the two swim categories, swim effort was standardized for swim speed. Mothers in echelon demonstrated significant increases in effort compared to periods of solitary swimming as evident by greater normalized tailbeat frequency

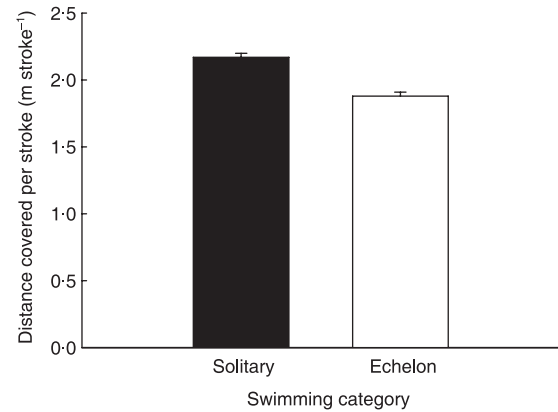


Fig. 4. ‘Infant carrying’ imparted maternal costs. Mother dolphins swimming in echelon with their calf (white bar) demonstrated significantly lower mean distance covered per stroke ($t = -7.068$, $P < 0.001$, $n = 178$, 156) compared to periods of solitary swimming (black bars).

($T = 19949.00$, $P < 0.001$, $n = 178$, 156) and reduced distance per stroke (Fig. 4). For a given speed, mothers swimming in echelon increased tailbeat frequency by 17%, which resulted in a 13% decrease in distance covered per stroke compared to solitary swimming.

Discussion

Infant carrying provides a solution for mothers who must locomote in their environment while accompanied by their young offspring. Echelon swimming in cetacean mother–infant dyads is a type of ‘infant carrying’ that improves calf swim performance (Noren *et al.* 2008), but it appears to come with a maternal cost. Average and maximum swim speeds were significantly slower for mothers swimming in echelon with their calves compared to periods of solitary swimming. For example, the mean maximum swim speed of the mothers swimming in echelon only represented 76% of the mean maximum performance of these mothers swimming solitarily. The maximum speed was assumed to represent the animal’s extreme performance, which is the method used to qualify physiological capacity (Weibel *et al.* 1987), thus this result implies that the presence of a calf is a detriment to maternal swim performance.

An alternate hypothesis for the decreased performance of dolphin mothers swimming in echelon is that the mother can only travel as fast as the infant can actively swim because the infant must occasionally stroke during the echelon swim behaviour. However, 0–1 month-old calves are capable of independent swim speeds of 0.58 – 4.20 m s^{-1} (Noren *et al.* 2006) and this performance is increased when the calf is in echelon (Noren *et al.* 2008) because it receives up to 60% of the thrust from its mother (Weihs 2004). Thus, it is unlikely that the swimming ability of an entrained calf constrains maternal echelon swim performance. Studies of chimpanzees (*Pan troglodytes*) also suggest that infant carrying decreases maternal travel speed (Wrangham 2000; Williams, Hsien-Yang & Pusey 2002).

In addition to decreased performance, dolphin mothers swimming in echelon were required to increase effort compared to periods of solitary swimming. For a given speed, mothers swimming in echelon significantly increased tailbeat frequency with the result that distance covered per stroke significantly decreased by 13% compared to solitary swimming (Fig. 4). Interestingly, the proportion of decreased distance per stroke in 'infant carrying' dolphin mothers is strikingly similar to the 17% decrease in distance per leap measured empirically for marmosets (*Callithrix jacchus*) carrying weights equivalent to their newborn twin offspring (Schradin & Anzenberger 2001). Furthermore, although female wallabies carrying a load (approximating the mass of a fully developed offspring) did not alter stride frequency, they increased the time the foot applied force on the ground, which likely increased the stored elastic strain energy to levels necessary to transport the additional load (Baudinette & Biewener 1998). Regardless of habitat (aquatic vs. arboreal) or forces to overcome (hydrodynamic drag vs. gravity) in these systems maternal effort must change to support an increased load.

The increase in maternal effort for dolphin mothers swimming in echelon compared to periods of solitary swimming may be associated with changes in water flow patterns and drag. The presence of the calf may disrupt the boundary flow around the mother causing it to separate, which would increase turbulent flow. In addition, the entrained calf could increase the surface area of the mother, which effectively increases the drag of the swimmer (Webb 1975). More power is required to overcome increased turbulent flow and drag (Webb 1975). As a greater proportion of maternal power output is utilized to accommodate increased turbulent flow and drag, there is less energy available to propel the animal forward. As a result, locomotor performance decreases because power output per stroke is limited by mechanical constraints (Fish & Hui 1991) and total work is limited by the animal's metabolic scope (Weibel *et al.* 1987). These relationships may explain the observed decrease in swim speed and distance covered per stroke for mothers swimming in echelon position. Although Weihs (2006) suggested that the gain in forward forces by the following body (calf) is larger than the added cost to the leading body (mother), a more detailed theoretical examination of the drag and flow patterns for the leading body in echelon position is warranted to validate the hypotheses for the proposed decreased maternal performance observed in the present study.

Given that infant carrying mothers must forage and evade predators, one of many constraints on newborn offspring mass may be its impact on maternal locomotor performance. As a result, newborn dolphins and marmosets represent a similar proportion of maternal mass, 15% (mass data from a mother–calf pair in this study) and 17% (Tardif, Harrison & Simek 1993), respectively. Ultimately as an infant ages and increases in size, maternal costs associated with infant carrying theoretically increase in aquatic (Weihs 2004, 2006) and arboreal (Schradin & Anzenberger 2001) environments. Optimal theory predicts that maternal carrying costs should not outweigh the sum of the costs of independent locomotion

by the mother and her offspring (Kramer 1998). Therefore, the transition to offspring locomotor independence may represent a parent–offspring conflict (Trivers 1974) as energy expenditure to carry an infant may limit the mother's available energy to invest in future offspring (Kramer 1998). As cetacean and primate offspring increase in size, there is an increase in the active prevention and/or avoidance of infant carrying by mothers in both groups (Altmann 1980; Taber & Thomas 1982; Mann & Smuts 1999), such that with age there is a decrease in the time cetacean infants swim in echelon (Taber & Thomas 1982; Mann & Smuts 1999; Noren & Edwards 2007) and primate infants are carried (Altmann & Samuels 1992; Salvage *et al.* 1996; Pontzer & Wrangham 2006). Examination of human infant carrying behaviour also suggests that by a certain mass and age, mothers encourage their infants to walk independently (Kramer 1998).

In summary, this study provides the first empirical evidence of the maternal consequences of 'infant carrying' in an aquatic environment. Although infant carrying provides a solution for mothers that must manoeuvre within their environment while accompanied by their underdeveloped offspring, this behaviour is associated with maternal costs regardless of environment, as evident in arboreal (Schradin & Anzenberger 2001) and aquatic (present study) regimes. The decreased locomotor performance and increased locomotor effort associated with infant carrying undoubtedly impacts maternal energy budgets, foraging efficiency and predator evasion. Given the prevalence of infant carrying behaviour across diverse taxa and habitats and the consequences of this behaviour, it is surprising that the energetics of infant carrying have largely been ignored. Future investigations are warranted, particularly in a volant environment, which remains unexplored.

Acknowledgments

I thank Dolphin Quest, particularly J. Sweeney and R. Stone, for providing the experimental facilities and animals and for funding portions of data collection and analyses. I also thank Southwest Fisheries Science Center (SWFSC), particularly S. Reilly and E. Edwards, for funding portions of data collection. In addition, I thank the staff at Dolphin Quest Hawaii (particularly G. Biedenbach and C. Buczyra), T. Williams of the University of California Santa Cruz for the use of her Peak Motus system, and J. Redfern of SWFSC for assistance with data management.

References

- Altmann, J. (1980) *Baboon Mothers and Infants*. Harvard University Press, Cambridge.
- Altmann, J. & Samuels, A. (1992) Costs of maternal care: infant-carrying baboons. *Behavioural Ecology and Sociobiology*, **29**, 391–398.
- Au, D. & Perryman, W. (1982) Movement and speed of dolphin schools responding to an approaching ship. *Fishery Bulletin*, **80**, 371–379.
- Baudinette, R.V. & Biewener, A.A. (1998) Young wallabies get a free ride. *Nature*, **395**, 653–654.
- Carrier, D.R. (1996) Ontogenetic limits on locomotor performance. *Physiological Zoology*, **69**, 467–488.
- Doran, D.M. (1992) The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study of paedomorphism and its behavioral correlates. *Journal of Human Evolution*, **23**, 139–158.
- Fish, F.E. (1993) Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology*, **185**, 179–193.
- Fish, F.E. & Hui, C.A. (1991) Dolphin swimming – a review. *Mammal Review*, **21**, 181–195.

- Kelly, H.R. (1959) A two body problem in the echelon swimming of porpoise. Naval Ordnance Test Station Technical Note 40606-1.
- Kooyman, G.L. & Ponganis, P.J. (1998) The physiological basis for diving at depth: birds and mammals. *Annual Review of Physiology* **60**, 19–32.
- Kramer, P.A. (1998) The costs of human locomotion: maternal investment in child transport. *American Journal of Physical Anthropology*, **107**, 71–85.
- Lang, T.G. (1966) Hydrodynamic analysis of cetacean performance. *Whales, Dolphins, and Porpoises* (ed. K.S. Norris), pp. 410–432. University of California Press, Berkeley.
- Mann, J. & Smuts, B. (1999) Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behavior*, **136**, 529–566.
- McBride, A.F. & Kritzler, H. (1951) Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. *Journal of Mammology*, **32**, 251–266.
- Noren, S.R. & Edwards, E.F. (2007) Physiological and behavioral development in dolphin calves: implications for calf separation and mortality due to tuna purse-seine sets. *Marine Mammal Science*, **23**(1), 15–29.
- Noren, S.R., Biedenbach, G. & Edwards, E.F. (2006) The ontogeny of swim performance and mechanics in bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology*, **209**(23), 4724–4731.
- Noren, S.R., Biedenbach, G., Redfern, J.V. & Edwards, E.F. (2008) Hitching a ride: the formation locomotion strategy of dolphin calves. *Functional Ecology*. doi: 10.1111/j.1365-2435.2007.01353.x.
- Norris, K.S. & Prescott, J.H. (1961) Observations on Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology*, **63**, 291–402.
- Pontzer, H. & Wrangham, R.W. (2006) Ontogeny of ranging in wild chimpanzees. *International Journal of Primatology*, **27**(1), 295–309.
- Rohr, J.R. & Fish, F.E. (2004) Strouhal numbers and optimization of swimming by odontocete cetaceans. *Journal of Experimental Biology*, **207**, 1633–1642.
- Ross, C. (2001) Park or ride? Evolution of infant carrying in primates. *International Journal of Primatology*, **22**(5), 749–771.
- Salvage, A., Snowden, P.T., Giraldo, L.H. & Soto, L.H. (1996) Parental care patterns and vigilance in wild cotton-top tamarins (*Saguinus oedipus*). *Adaptive Radiation of Neotropical Primates* (eds N.A. Norconk, A.L. Rosenberg & P.A. Garber), pp. 187–199. Plenum Press, New York.
- Schradin, C. & Anzenberger, G. (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: an experimental analysis. *Animal Behavior*, **62**, 289–295.
- Skrovan, R.C., Williams, T.M., Berry, P.S. & Moore, P.W. (1999) The diving physiology of bottlenose dolphins (*Tursiops truncatus*) II. Biomechanics and changes in buoyancy at depth. *Journal of Experimental Biology*, **202**, 2749–2761.
- Taber, S. & Thomas, P. (1982) Calf development and mother–calf spatial relationships in southern right whales. *Animal Behaviour*, **30**, 1072–1083.
- Tardif, S.D., Harrison, M.L. & Simek, M.A. (1993) Communal infant care in marmosets and tamarins: relation to energetics, ecology, and social organization. *Marmosets and Tamarins: Systematics, Behavior, and Ecology* (ed. A.B. Rylands), pp. 200–219. Oxford Press, Oxford.
- Tavolga, M.C. & Essapian, F.S. (1957) The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): mating, pregnancy, parturition and mother–infant behavior. *Zoologica*, **42**, 11–31.
- Trivers, R. (1974) Parent–offspring conflict. *American Zoologist*, **14**, 249–264.
- Webb, P.W. (1975) Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board of Canada*, **190**, 1–159.
- Weibel, E.R., Taylor, C.R., Hoppeler, H. & Karas, R.H. (1987) Adaptive variation in the mammalian respiratory system in relation to energetic demand: I. Introduction to problem and strategy. *Respiration Physiology*, **69**, 1–6.
- Weihs, D. (2004) The hydrodynamics of dolphin drafting. *Journal of Biology*, **3**(8), 1–23 (<http://jbiol.com/content/3/2/8>).
- Weihs, D. (2006) Aerodynamic interactions between adjacent slender bodies. *American Institute of Aeronautics and Astronautics Journal*, **44**, 481–484.
- Wells, J.P. & Turnquist, J.E. (2001) Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): II postural and locomotor behavior and habitat use in a free-ranging colony. *American Journal of Physical Anthropology*, **115**, 80–94.
- Williams, J.M., Hsien-Yang, L. & Pusey, A.E. (2002) Costs and benefits of grouping for female chimpanzees at Gombe. *Behavioural Diversity in Chimpanzees and Bonobos* (ed. C. Boesch), pp. 192–203. Cambridge University Press, Cambridge.
- Wrangham, R.W. (2000) Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. *Primate Males, Causes and Consequences of Variation in Group Composition* (ed. P.M. Kaepler), pp. 248–258. Cambridge University Press, Cambridge.

Received 12 June 2007; accepted 27 September 2007

Handling Editor: Francisco Bozinovic